No. 6. — *Migrations of New England Bats*

By Donald R. Griffin

The phenomena associated with bird migrations are among the most complex and inexplicable to be found in biology. Consider for example the golden plover; the mere statement of its migration routes presents a challenge to the biologist. How can this small shorebird find its way from Alaska to the Hawaiian Islands over 2000 miles of open ocean — and how can the young birds make their way from the Arctic Ocean to the Argentine on their first flight, in some cases, *without older birds to guide them?* (Clark, 1905; Henshaw, 1910; Lincoln, 1935).

Other fundamental problems are raised by recent experiments demonstrating the influence of light on the anterior pituitary, and indirectly on the gonads and on migration. (Rowan, 1931; Bissonette, 1938; and Benoit, 1936). The related problem of homing and distant orientation has also received attention (Rüppell, 1935, 1936 and 1937; Watson and Lashley, 1915), and here too much remains to be explained.

It is not the purpose of this paper to discuss the problems of bird migration, but the far-reaching nature of these problems justifies, in my opinion, a careful study of all related phenomena, such as the homing behavior and migrations of other animals.

The word "migration" is sometimes used loosely to cover many different types of animal movements. It seems best to restrict the term to the regular, periodic movements of a population to a new environment and their return to the area from which they started, the period of a complete cycle usually being one year. Only true migrations in this sense will be considered here.

Bats are the only living vertebrates, other than birds, which fly, and there is a considerable body of evidence to indicate that some of them migrate. In this paper I shall review this evidence and present the results of a banding study of New England bats in which I have been engaged during the past six years. During this period I have banded 11,739 bats of six species in New England and eastern New York State, and over 2000 recaptures of banded bats have been recorded.

It is impossible to acknowledge here all the assistance I have received in the course of the actual banding. Only with the assistance of several other college students was it possible to handle this number of bats on weekend and vacation trips to caves and mines, which are often located in regions difficult of access. The following have joined me on several of these trips and I wish to express my gratitude for their indispensable aid: Frederick L. Osgood of Rutland, Vt., Thomas L.

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The bats of New England are fairly typical of those of the temperate parts of the Northern Hemisphere, and this paper will be concerned primarily with them, not because they are intrinsically more important than the bats of any other region, but because my own experience has been confined to the northeastern United States. The problems are not local, and evidence obtained in one part of the world is applicable with reservations to the study of bats in any other area of similar climatic conditions.

Nine species and sub-species of bats have been recorded from the New England States, and all of them belong to the family Vespertilionidae. They were divided by Merriam (1887) on the basis of their habits into two groups, the cave bats and the tree bats. The forms found in New England are closely related, and this grouping is based on behavior and ecology, not on morphological or taxonomic differences.

Cave bats hibernate in caves during the winter, and they often spend the daytime in buildings or hollow trees during the summer. Some are very gregarious, and three or four hundred may congregate in the crevices in the loose trim of a single building, while a large cave may contain thousands. (Sherman, 1929; Allen, 1921; Banta, 1907; Bailey, 1928 and 1931; Hahn, 1908; Blatchley, 1896; and Mohr, 1933). These large summer colonies usually contain only females and their young which are born in June. This habit of congregating in breeding colonies (or *Wochenstuben* = maternity wards) is apparently common to the genus *Myotis* in both Europe and North America (Eisentraut, 1934 and 1936; Barret-Hamilton, 1910; Griffin, 1934 and 1936; and Sherman, 1929).

The following species classed as cave bats are found in New England:

Eptesicus f. fuscus (Beauvois), the big brown bat
Myotis l. lucifugus (LeConte), the little brown bat
Myotis sodalis Miller and Allen, the cluster bat or pink bat
Myotis keenii septentrionalis (Trouessart), the Say bat
Myotis subulatus leibii (Aububon and Bachman) the least brown bat
Pipistrellus subflavus Miller, the pipistrelle

The last four are not common in New England, and no very large breeding colonies of these species have been reported, although they all pass the winter in New England caves.

The tree bats are seldom found in caves (Merriam, 1887; Rhoads, 1903; Mohr, 1932c), and apparently they are not nearly so gregarious as the cave bats. They are not found in large summer colonics in buildings, and they normally spend the daytime singly or in small groups in trees.[1] There is one record of several young bats, uncertainly identified as the silver-haired bat, *Lasionycteris noctivagans*, being found in an old crow's nest (Merriam, 1884). The tree bats found in New England are:

Lasiurus borealis (Müller), the red bat
Lasiurus cinereus (Beauvois) the hoary bat
Lasionycteris noctivagans (LeConte), the silver-haired bat

Both cave bats and tree bats feed exclusively on flying insects, and in climates like New England's this source of food is practically non-existent during the winter months. Therefore one can reason *a priori* that all these bats must either (a) migrate south to regions where insects are available throughout the year, (b) find other sources of food, (c) store food, or (d) hibernate. All who have studied bats most closely agree that in their natural state the species found in the eastern United States eat nothing but insects. (Seton, 1910; Hahn, 1908; Barret-Hamilton, 1911). Nor does insect food lend itself to storage. Apparently such food is usually caught on the wing, and is either eaten while the bat is flying or while it is hanging from an elevated support. Under such circumstances, pieces of prey once dropped are lost for good. This seems to have had its effect on the feeding habits of the animals, for even in captivity they lose all interest in a morsel of food, if it once drops from their mouth. (Hahn, 1908.)

Migrations of Tree Bats

Merriam (1887) was apparently the first to point out that the three species of tree bats breed in the transition, Canadian and boreal faunal zones of North America,[2] and yet that they are never found hibernating in caves. In winter these bats are regularly taken far south of their summer range. Merriam mentions a hoary bat taken at George-

[1] See footnote on page 220.
[2] For a discussion of Faunal Zones and Indicators see Merriam (1898).

town, S. C., in January, 1887 and another from Savannah, Georgia in February of 1886, while Miller (1897) reported one killed at Brownsville, Texas in late October. More recent collections would swell the list, but the general picture remains the same for all three tree bats; a northern breeding range from which the bats are absent in winter, and a southern winter range, where the hoary and silver-haired bats are not found in summer.[1] The red bat breeds over a large area, including part of its winter range, so that one cannot notice sharp differences in its seasonal distribution. (Stephens 1906; Seton 1909.)

Merriam reported (1887) that silver-haired bats appeared every spring and fall at Mt. Desert Rock, 30 miles from the Maine coast and 15 miles from the nearest island. Bats of any kind were unknown on this barren rock at other seasons. Miller (1897) reported that all three species of tree bats appeared in autumn at Highland Light, Truro, Mass., on the tip of Cape Cod. Tree bats have not been reported on the dry infertile lower Cape during their breeding season, and it seems most likely that the small flocks reported by Miller were migrating south along the coast. Saunders (1930) reported that hoary and silver-haired bats flew against a lighthouse on Lake Erie along with migrating birds. Howell (1908), Rhoads (1903) and Mearns (1898) have reported flocks of bats seen flying during the daytime — evidently in migration.

Furthermore there are several records of tree bats alighting on ships some distance from land during the autumn months. No one of these records alone would be of any extreme significance, but when taken together they present an impressive picture. Allen (1923) reports that a flock of unidentified bats alighted on a ship "10 miles off the Delaware River" in September, 1902, according to a newspaper account. Nichols (1920) reports that a red bat boarded a ship between

[1] The description here presented of the habits of tree bats seems to be the typical one, based on the reports of recent observers. Like any set of rules for animal behavior there are bound to be occasional exceptions. Thus Hahn (1908) reports skulls of *Lasiurus cinereus* and *Lasiurus borealis* found in caves, indicating that in the past these species may have had different habits. Godman (1842) quotes a report that red bats were found hibernating in caves south of Albany, New York, but unfortunately the identification was not certain and no specimens were taken. I have visited caves in this region without ever finding a single tree bat among hundreds of the cave dwelling species. Merriam (1884) speaks of the silver-haired bats inhabiting caves although he does not specifically mention ever finding one below ground. Seton (1909) writes that the red bat is "known to gather in vast numbers in caves of its more southerly range" but gives no authority. Stone and Cram (1903) make the same statement, likewise without authority. Like Mohr (1932c) the writer is "skeptical of cave records (of tree bats) not verified by specimens".

There are a few records of large colonies of tree bats in houses. Stone and Cram describe (1903, p. 203) a colony of red bats in the attic of a house. Merriam (1884) quotes a letter from William Brewster saying that lumbermen told him of finding bats *in winter* in logs brought in for firewood. This was not Merriam's own experience (1887), and on a subject where confusion of dates and exact circumstances is so apt to arise popular reports are notoriously unreliable.

All of these records run counter to the weight of evidence accumulated by more recent observers, and it seems that they must represent atypical cases. Furthermore none of them is backed by specimens to my knowledge. After all it is the normal behavior of animals in which we are interested, not the exceptions.

Diamond Light Ship and the Capes of the Carolinas on September 3, 1919. Haagner (1921) records that on September 1, 1920 a red bat was found on a ship inbound from South Africa, when she was three days out of Philadelphia. In this case there was no possibility that the bat had accompanied the ship away from the coast. Murphy and Nichols (1913) observed a bat, probably a silver-haired bat, five miles off Sandy Hook, N. J. on September 6, 1907. MacCoy (1930) reports a bat taken five miles N.N.W. of Provincetown, Mass. August 18, 1929, when it boarded a fishing vessel. Thomas (1921) collected two silver-haired bats and one red bat out of a flock of about 100 which "caught up with the ship twenty miles off the coast of North Carolina" on September 3, 1920. Finally Norton (1930) records that a red bat was taken on a ship at 42° N. latitude, 66° W. longitude, 240 miles east of Cape Cod and 130 miles S. × W. of Cape Sable, Nova Scotia on August 17th, 1929. Two additional records of bats at sea have recently come to my attention. Mr. D. F. Bumpus has presented to the Museum of Comparative Zoölogy three silver-haired bats which he captured on the *Atlantis* on August 25, 1938 at 39° 09′ N. lat., 70° 22′ W. long. (130 miles S. × E. of Nantucket Island, Mass.). Dr. N. T. Werthessen of the Boston Dispensary saw a bat at 45° 07′ N. lat. 42° 36′ W. long. on September 7, 1937 while eastbound on the S. S. American Banker. The bat flew within 15 or 20 feet but could not be captured. This bat was about 500 miles from Cape Race, Newfoundland, the nearest land. The ship was about 85 hours out of New York, and as the bat had not been seen previously it seems unlikely that it had been carried from New York on board the vessel. Small migrating land birds behave in exactly the same manner, and all of these records would be exceedingly difficult to explain, unless we assume that the tree bats are migrating down the coast in late August and September.

Allen (1921) gives evidence indicating that the tree bats are found in Bermuda during the autumn months but not at other seasons. In view of their usual northern breeding range it is very unlikely that the hoary and silver-haired bats breed in Bermuda. Jones (1884) writes as follows of the hoary bat, *Lasiurus cinereus:*

"According to the observations of Mr. J. L. Hurdis . . . who passed 14 years upon the islands . . . and during that lengthy period was a close observer of the habits of all animals which came under his notice, only two species of bat are known to visit the Bermudas, and that usually in the autumn and early months of the winter. The present species is observed occasionally at dusk during the autumn months . . .

but as it is never seen except at that particular season it is clear that it is not a resident . . . ."

If the tree bats do migrate between the mainland and Bermuda they must fly over 600 miles of open ocean.

Unfortunately the North American tree bats do not lend themselves to successful banding studies, which require that large numbers of individuals be marked in order that a few may later be recovered. These bats are neither numerous nor colonial, so that large numbers cannot be captured. However, Eisentraut (1936, 1937) was able to band 600 Noctules, *Nyctalus noctula*, a European genus not represented in the United States, but somewhat similar in its habits to the American tree bats. The noctules are large bats and strong fliers, but they are sufficiently gregarious that the 600 could be caught in a single building in Dresden, Germany, where they were spending the winter. Five of these bats were retaken later, all of them having flown north from their winter quarters. The most distant recovery was from a point in Lithuania 475 miles from Dresden. This seems to prove conclusively that the European *Nyctalus noctula* is capable of long migratory flights.

The indirect, circumstantial evidence discussed above is exactly paralleled by the behavior of migrating birds. They appear temporarily in large numbers at points along their route where they are unknown at other seasons, and they often alight on ships off the coast. Thus while we lack direct, conclusive banding evidence, it seems an almost inescapable conclusion that the North American tree bats perform annual migrations of several hundred miles to reach regions where insect food is available throughout the winter.

Migrations of Cave Bats

Cave bats, of which the most common is *Myotis l. lucifugus*, the little brown bat, are found throughout the United States and Canada up to the northern limits of the forests. Although they need not fly south in winter to a warmer climate, they must find suitable retreats in which to hibernate. These requirements for hibernation will determine their winter distribution.

Caves are certainly the typical hibernation quarters for bats. They remain at a low and constant temperature throughout the winter, and if they are large enough the bats are never subjected to freezing temperatures, which hibernating mammals can seldom survive (Johnson 1931; Merzbacher 1903; Rulot 1902). I have found that two hibernating *Eptesicus f. fuscus* were killed if placed in an ice box where the temperature was about −5° C. Furthermore caves are usually very humid and this is an advantage if not a necessity, for bats kept in hibernation in a cold room will die of desiccation if some provision is not made to keep their surroundings nearly saturated with water vapor. Mine tunnels are equally suitable, of course, and many of the largest bat colonies in New England are in abandoned mines.

There are several records of bats hibernating in other situations. Johnson (1933) kept five *Eptesicus f. fuscus*, the big brown bat, hibernating in a room where the temperature was between 45° and 57° F. (average 51° F.). These bats lived a little over two months, but died in January having lost almost 50% of their weight. Swanson and Evans (1936) writing of Minnesota cave bats, record several instances where *Eptesicus f. fuscus* spent the winter in buildings. Mearns (1898) says of the little brown bat in the Hudson Highlands of New York, "I have found it dormant in hollow trees in winter." The writer found a group of Say bats, *Myotis keenii septentrionalis,* apparently hibernating in a well during December. During the winter months many bats are reported flying about in cities and inside large buildings. Most of these are big brown bats *Eptesicus f. fuscus,* which are apparently hardier than the smaller and more abundant *Myotis l. lucifugus.* Guthrie (1933) reports, (and I have noticed the same point) that *Eptesicus f. fuscus* is usually found in the colder, more exposed parts of caves, near the entrances for instance.

There are so many *Eptesicus* found each winter in the city of Boston that it seems certain that they must hibernate in heated buildings, finding, perhaps, some retreat where the temperature remains low and fairly constant. Wetmore (1936) kept an *Eptesicus* in an exposed but somewhat insulated box at Washington, D. C. all winter. The bat survived despite the fact that the temperature inside the box varied from −14° to 15.6° C. Swanson and Evans (1936) also report that *Eptesicus* hibernated successfully for three weeks at 27.6° F.

When one tries to keep bats hibernating in captivity it seems that the requirements for successful hibernation must be very restricted, especially for the smaller cave bats (genera *Myotis* and *Pipistrellus*). The temperature must be above freezing, but the bat's metabolic rate must not be so high that all its fat reserves oxidize before the winter is over. This seems to have been the fate of the *Eptesicus f. fuscus* which Johnson (1933) kept at an average of 51° F. The humidity must be high, but not complete saturation. It is difficult to imagine how these exacting requirements can be met during extreme fluctuations of winter temperature except in inclosed spaces below ground. I have never found bats hibernating in mid-winter in caves less than 25 feet long and about five feet high. If such caves are not suitable, how can bats survive in retreats with such poor insulation as buildings, hollow trees or small crevices in the rocks? Certainly most of the bats found outside of caves in winter are in poor condition, and it is always possible that the bats which appear in winter in towns have chosen unsuitable hibernation quarters and are driven out by adverse conditions.

Except for *Eptesicus f. fuscus* it seems that very few of our cave bats hibernate successfully outside of caves or mines. This is not proven by any means, and the habits of bats have been studied so little that it is possible that some one may discover large numbers of them hibernating in totally unsuspected places. As will be made clear below, the banding evidence on the movements of cave bats throws some light on this problem.

Observation of cave bats had long ago led to the belief that they might be migratory. The typical summer colonies in buildings are deserted in winter (Sherman, 1929; Griffin, 1934; Eisentraut, 1934, 1936; Barret-Hamilton, 1910; Hugues, 1912). Caves in New England, although well populated with hibernating bats in winter are practically deserted during the summer months. Hahn (1908) and Mohr (1932c, 1933) noted fluctuations in the population of caves in Indiana and Pennsylvania respectively. They were led by this indirect evidence to believe that seasonal migrations were in progress, although it was not possible to trace them very definitely. Hugues (1912) and Casteret (1938) in France noted apparent shifts in the bat population from caves to summer colonies. Zimmerman (1937) reported the sudden appearance of a great concentration of *Myotis l. lucifugus,* suggesting that a mass movement of some sort was under way.

Guthrie (1933) studied seasonal fluctuations in the bat populations of two Missouri caves. *Myotis grisescens,* the little gray bat, (not found in New England) apparently wintered elsewhere but passed through the region studied "towards the end of April, but did not become a cave resident except temporarily at that time". A few weeks later, however, *Myotis grisescens* returned to the caves in large numbers and remained during the summer months. *Myotis sodalis* spent the winter in the caves in large numbers, but moved about considerably, apparently in correlation with changes in temperature. During the summer this bat left the caves altogether. *Myotis l. lucifugus* hibernates in the caves but leaves them for the summer.

This summary indicates the type of results which have been ob-

TABLE 1. CAVE BATS BANDED IN THE NEW ENGLAND REGION

Species	*N. H.*	*Vermont*	*Mass.*	*Conn.*	*New York*	*Total*
Eptesicus f. fuscus	39	38	56	34	8	165
Myotis l. lucifugus	178	1823	3735	1053	862	7651
Myotis keenii septentrionalis	...	141	614	266	123	1144
Myotis sodalis	...	2032	72	252	14	2370
Myotis subulatus leibii	...	10	....	1	....	11
Pipistrellus subflavus obscurus	...	60	70	149	119	398
Totals	217	4094	4547	1755	1126	11739

tained by direct observation of bat populations. It is evident that large scale movements are occurring, but the evidence obtained is limited.

If the vast majority of cave bats must hibernate in caves, natural or artificial, those which spend the summer in areas where there are no caves must obviously migrate to caves in another region. Eastern New England is an example of an area where caves large enough to shelter hibernating bats are practically non-existent. Since there are in western New England several caves where bats winter by the hundreds, it is logical to assume that an annual migration takes place between the two areas.

In 1932 I became interested in this problem, and realized that by banding large numbers of bats at both caves and summer colonies it might be possible definitely to demonstrate such a migration if it occurred. Since cave bats are colonial both in summer and winter, they can be banded in quantities that are out of the question with the far less abundant tree bats. It was felt that if such a migration could be demonstrated it would show that even the smallest of our bats and the weakest fliers were capable of long migratory flights (for summer colonies are sometimes several hundred miles from the nearest caves). In addition to its intrinsic interest, the proof of such a migration would be good indirect evidence for the longer migrations ascribed to the tree bats.

Methods and Procedure

The methods used were in principle very simple. Bats were caught and banded, complete records kept, and the recaptures of banded bats on subsequent visits to the colonies were tabulated and analysed. Since the area to be covered was large, the chance that bats would be retaken at a distance would have been vanishingly small, unless a very large number were banded. To date over 50 bats have been retaken at a different colony than the one where they were banded. Many of these had traveled no great distance, but others yielded significant records which will be presented below. Table 1 shows the numbers of each species banded in various states.

Practically all the bats were banded with No. 1 aluminum bird bands kindly furnished by the U. S. Bureau of Biological Survey. These bands, like all the bird bands used in the United States, bear a serial number on the outside and on the inside the inscription "Notify Biol. Surv. Wash. D. C." This is sufficient postal address for the Bureau, and any one finding a banded bird or bat is expected to send the band or report the number to this Bureau, which keeps complete files showing when and where all bands were used. Many birds are reported each year by persons who accidently find them dead, but bats are so retiring in their habits and there is so much popular aversion to them that only 18 returns have been secured in this way. The most interesting recoveries have been obtained when banded bats were retaken at other colonies in the course of the regular banding work.

The bands are applied by closing them around the bat's hind leg and pinching them against the interfemoral membrane. A properly applied band, which is tight and does not move, seldom seems to injure the bats, and the high number of recoveries sometimes obtained shows that the method is fairly satisfactory. Often 80 or 90 percent of the bats banded in autumn in a cave will be retaken in the same cave later the same winter, showing that no very large mortality or loss of bands occurs. Plate 1 shows a bat with the band in position.

Other bat banders have sometimes used different methods. Eisentraut (1934) places aluminum bird bands around the bat's humerus. This method has the advantage that the band can be seen when the bats are in a compact cluster, whereas leg bands are only visible when the bats are handled individually. Hibernating bats hang head down from the rock, and they often form thick clusters like those shown in Plates 1 and 2 where there may be two or three hundred bats per square foot of rock surface. It has always seemed to me that the possibility of injury to the wing was serious, whereas slight damage to a leg is not so apt to be fatal. Mohr (1934) uses fingerling tags placed on the bats' ears, and this method also has the advantage of easy recognition. However the tags are so small that no return address can be stamped on them, and they are relatively expensive. Mohr (personal communication) has some fears that the tags may injure the bats, although my experience suggests that there is little to choose between the three methods. I have marked about 160 bats with wing bands and ear tags, and the percentage retaken has been as high or higher than with bats bearing leg bands.

The actual catching of bats is easy in caves. The bats are usually dormant and can be plucked from the walls by hand or with a net if out of reach. Often they retire into small deep crevices or into drill holes in mines and they must be extracted from such retreats with long metal forceps. Summer breeding colonies in buildings present more difficulties. Usually the bats spend the daytime inside the trim of frame buildings or in cracks between the rafters and roof boards. In most cases it is impossible to dislodge them without seriously damaging the building itself. Therefore means had to be devised to catch the bats as they voluntarily left their roosts for the night's hunting.

One useful method was to nail U-shaped wire supports over the holes from which the bats emerged and to stretch cheese-cloth over this frame work, forming a tunnel of netting which could be led down to within reach of the ground. Typical "tunnel nets" of this type are shown in Plates 2 and 3. When the bats emerge they are presumably hungry, and perhaps the ones behind are pushing; at any rate they come with a rush and apparently do not see the netting until they strike it. Probably they are not expecting obstructions immediately below the hole they have flown out of so often. The bats will usually drop to the bottom of even long nets such as are shown in Plates 2 and 3. The one shown in Plate 2 caught 250 in a single evening.

These tunnel nets were so successful that an unexpected difficulty was encountered. The bats came so fast (200 in twenty minutes) that they could not be removed and placed in ordinary cages. Too much time was needed to open and close a cage door, or to open and close a bag without allowing the bats already inside to escape. Therefore an entirely new type of container was developed which had an opening at the top surrounded by smooth sheet metal so that the bats could not crawl up to the opening (see Plate 4). Since the bats cannot fly in the small space inside the container, the hole need not be closed and one can reach in at any time without fear of releasing bats already inside. The best size for these containers proved to be about 12 inches in diameter and 15 inches high. The metal tops must be absolutely smooth, without seams or rough spots. They can be made very economically from small milk strainers with the strainer netting removed.

By placing a cylindrical container of this sort with a relatively larger opening under a short tunnel net of cheese-cloth it is possible to make an automatic bat trap which will catch the bats as they leave their holes and will not require constant tending. Recent experience has shown that these traps can be greatly improved by making the smooth upper section of transparent celluloid. This is not so conspicuous as netting or sheet metal and the bats enter such a trap more readily. Plate 5 shows one of these celluloid traps in position. These bat traps are shown in Plates 3 and 4. Four such traps, covering the principal exits by which bats left the building shown in Plates 2 and 4, took 350 bats in one evening. When the bats use many holes in a building it is best to plug with newspaper or cloth those holes not covered by traps.

From a knowledge of bird migrations it is possible to predict what one might expect if cave bats do have definite annual migrations from caves to distant summer colonies. Migratory birds usually return each year to the same breeding area, although this in itself is no proof of migration, as a resident population might also be found each year in the same breeding grounds. In addition migratory birds always seem to have a well developed "homing instinct". If they are carried away, they tend to return sooner or later to the place where they were originally taken. The development of a good homing ability seems to be correlated with the habit of migration. Thus if New England cave bats were migratory we might expect to find: (a) that a large proportion of them returned each year to the same caves and breeding colonies, (b) that if bats were artificially carried away from the caves or buildings where they were caught, they would return, and (c) that some which were banded in caves would later be retaken in summer colonies or *vice versa*. It is pertinent to consider the recoveries of banded bats which have been obtained by various investigators from these points of view.

Terminology will be borrowed from bird banding to describe different types of recoveries of banded bats. A *return* is any recapture of a banded individual at another locality, or a recapture at the same locality where it was banded, after the passage of a season when the animals are believed to be migrating. If the bat has moved from one locality to another it is called a *foreign return*. If it is retaken at the point where it was banded after a seasonal absence, it is known as a *local return*.

(a) *Local returns*.

In 1916 (the earliest bat banding on record) A. A. Allen (1921) marked four female *Pipistrellus subflavus* which had been caught in a building at Ithaca, N. Y. Three years later three of the four were retaken in exactly the same spot. Mohr (1934, 1936) and Poole (1932) have marked several hundred bats in Pennsylvania, and the percentage of local returns was 20% to 40%, Eisentraut (1934, 1935, 1936) has banded about 6000 European cave bats, mostly *Myotis myotis*, in caves near Berlin. He found that the percentage of local returns was about 30%. In certain parts of the caves where most of the bats could be captured, the percentage was sometimes as high as 50%.

At two caves in Vermont where it is possible to catch all the bats, I have retaken an average of 36.7% and 56.8% respectively during the two winters following the date of banding. These figures include both *Myotis l. lucifugus* and *Myotis sodalis*. These percentages are variable and would be higher if it were not so difficult to catch all the bats in a colony. The influence of bats overlooked and of the natural mortality is discussed in Appendix I. The important point to keep in mind is that if every surviving bat returned, the fraction of them most likely to be retaken will be the *product* of the fractions of the total number present which are taken on each visit. As explained more fully in Appendix I the percentages quoted above probably indicate that a substantial proportion of the bats surviving the summer return each winter to the same cave to hibernate.

At summer colonies the percentages recovered are lower, both because it is much more difficult to catch all the bats in a building,[1] and because the bats are more likely to move from one summer colony to another. . . . Of 1047 *Myotis l. lucifugus* banded at summer colonies on Cape Cod, Mass., 111 or 10.5% have been retaken later at the same building. This should be compared with an average percentage of 25% to 30% local returns to caves. At summer colonies an average of 13.4 out of every thousand *Myotis l. lucifugus* banded were retaken as foreign returns at another colony a few miles distant, while there were only 1.7 foreign returns recorded out of every thousand bats banded in caves.[2]

Thus the New England cave bats seem to have a definite tendency to return successive years to the same colony, and this tendency is more highly developed at the caves than at the summer colonies in buildings.

(b) *Homing Experiments.*

Almost every bat bander has carried some bats to a distance from their home roost before releasing them; (see Howell and Little (1924), Mohr (1934), Eisentraut (1934, 1936), Casteret (1938). I have summarized the results of all homing experiments in tabular form in Table 2 in so far as the data at hand permit. To shorten the table I have grouped together the bats from the same colony released at the same point, even though they may have been transported during different seasons. The last column of the table requires some explanation. It is

[1] Using the terminology developed in Appendix I, c_1 and c_2 are small, so that P is much smaller than F.

[2] The majority of bats which have been recorded as foreign returns moving from one cave to another originated in a cave at East Dorset, Vt. This cave has a very large entrance and it evidently becomes too cold for bats in mid-winter. Although three or four hundred bats may be found there in November, there have never been nearly so many in April. A few dead bats are always found in late winter, sometimes frozen into the large stalactites and stalagmites which grow up in the cave as ground water seeps through the roof and freezes. Evidently the bats which try this cave one winter are very likely to move elsewhere if they survive. Only 18 bats banded in this cave have been recorded as returns of any sort, and 10 of these 18 were foreign returns. If this cave is neglected as atypical, the number of foreign returns per thousand bats banded falls to 0.7.

(S) = summer colony; (W) = cave

Species	*Locality Captured*	*Experimenter*	*Distance transported (miles)*	*Number transported*	*Number Retaken*	*% of transported bats retaken*	*% of local releases retaken*
Eptesicus f. fuscus	Covina, Cal. (S)	Howell and Little (1924)	20	5	2	40.0%	.....
" " "	W. Andover, Mass. (S)	Griffin	19	6	5	83.3%	57.7%
Myotis myotis	Berlin, Germany (W)	Eisentaut (1936)	26	40	9	22.5%	32.8%
" "	" "	"	95	22	1	4.5%	32.8%
Miniopterus schreibersii	Hautes-Pyrenees, France (S)	Casteret (1938)	10	138	42	30.4%	.....
M. schreibersii & Myotis myotis	" "	"	21	66	18	27.3%	.....
M. schreibersii & Myotis myotis	" "	"	62	115	6	5.2%	.....
Myotis myotis	" "	"	10	1	1	100.0%	.....
" "	" "	"	124	17	1	5.9%	.....
Myotis l. lucifugus	Kempton, Penn.	Mohr (1934)	1 to 30	51	12	23.5%	.....
" " "	Kutztown, Penn.	Poole (1932)	18	10	6	60.0%	.....
" " "	Pricetown, Penn. (S)	"	10	20	4	20.0%	.....
" " "	Hatchville, Mass. (S)	Griffin	12	22	4	17.4%	10.5%
" " "	" "	"	3	9	2	22.2%	14.7%
" " "	" "	"	33	2	1	50.0%	27.2%
" " "	Mashpee, Mass. (S)	"	10	140	17	12.1%	11.5%
" " "	" "	"	12	2	0	0	11.5%
" " "	" "	"	36 (at sea)	24	6	25.0%	14.4%
" " "	" "	"	24	5	1	20.0%	8.1%
" " "	" "	"	66	49	2	4.1%	8.1%
" " "	Cotuit, Mass. (S)	"	12	45	10	22.5%	25.6%
" " "	" "	"	3	10	3	30.0%	25.6%
" " "	Chittenden, Vt. (W)	"	20	10	2	20.0%	50.0%
Myotis sodalis	" "	"	20	35	10	28.6%	23.8%
Myotis l. lucifugus	Roxbury, Conn. (W)	"	156	82	7	8.5%	30.7%
Myotis sodalis	" "	"	156	44	2	4.5%	31.4%

valuable for comparative purposes to know how many of the bats from a given colony, *which were released where they were caught,* were later retaken. These bats are spoken of as "local releases," and they constitute the majority of the bats banded. The percentage of local returns from the local releases varies widely, but the significant point, in my opinion, is that in almost every case the bats which I have released at a distance were as likely to be retaken as the local releases. This is shown graphically in text fig. 1, where the solid bars represent local releases and the outlined bars show the percentage of transported bats retaken.

The fact that in almost every case more transported bats were retaken than local releases is worth noting, but is probably not significant. The base of text fig. 1 shows that this difference was fairly sizeable, when all the bats from different colonies are totalled together. The process of being banded probably frightens and disturbs the bats, and when released locally many of them desert the roost where they were caught and move to another colony. For some reason those carried to a distance seem to be less likely to associate the discomfort of being banded with the home roost.

The relation between distance transported and percentage retaken is interesting, but the data available are insufficient to warrant definite conclusions. Only when the distance transported exceeded 50 miles did the percentage retaken fall far below the control figure afforded by the local releases.

None of my homing experiments give any precise indication of the speed of homing. Usually I did not visit the colonies more than two or three times during the summer, as too much attention causes the bats to move elsewhere. Therefore most of these homing returns were obtained during subsequent seasons. A few bats transported short distances have been retaken at their home colony during the same season, and one carried 66 miles away was retaken ten weeks later at another summer colony two miles distant from where it had been caught and banded. Mohr (1934) records 3 bats which returned 30 miles in 12 days.

In the case of the big brown bat, *Eptesicus f. fuscus,* I have one rather surprising homing record. Five bats of this species were transported 19 miles, photographed and released (one of them is shown in Plate 1). In spite of considerable rough handling which they received, every one was retaken when their home roost was revisited 36 days later.

There are two records at hand of bats which were transported and were later retaken at points on a direct line between the place of cap-

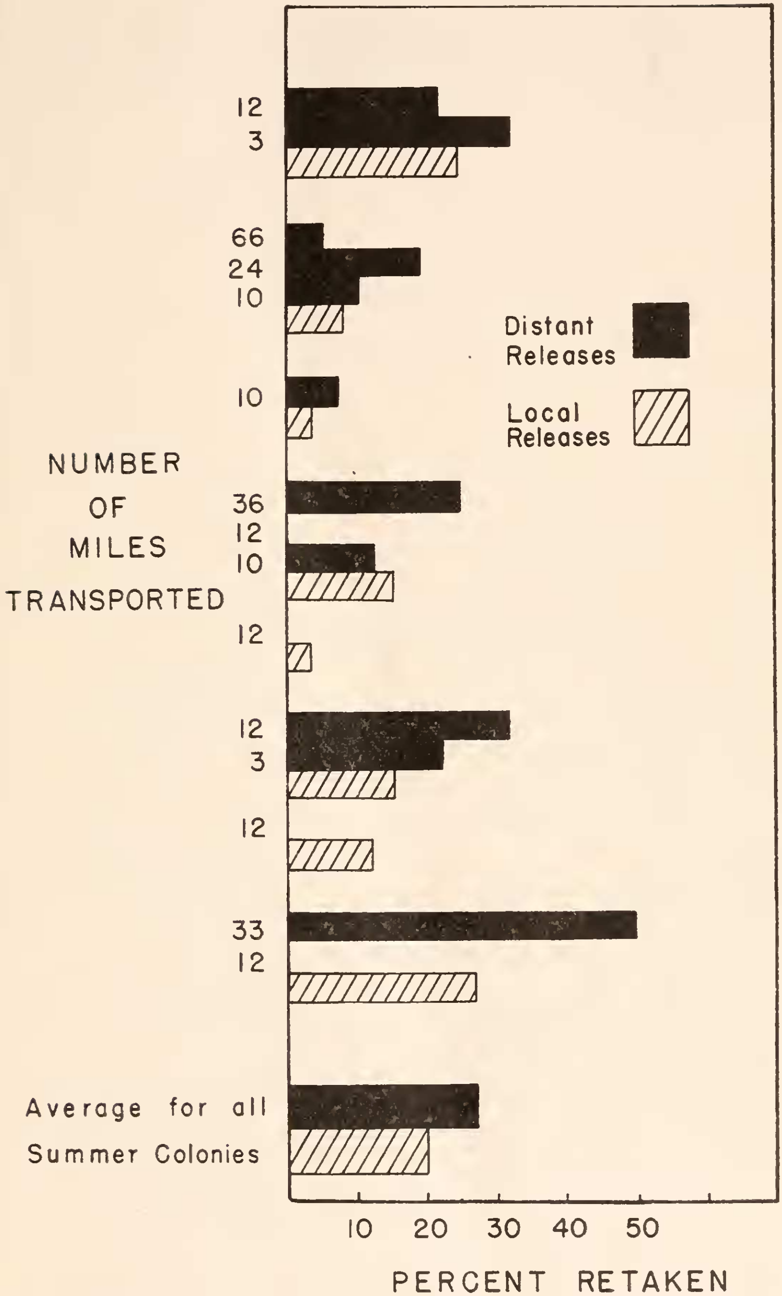
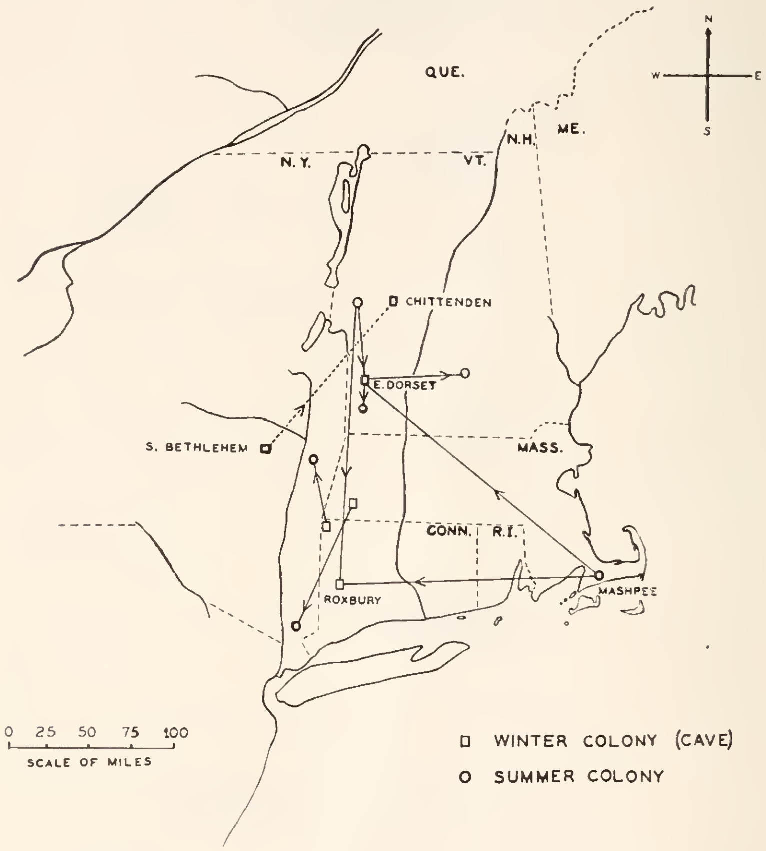


Fig. 1. Recoveries at home roost of local and distant releases of *Myotis l. lucifugus* from various summer colonies on Cape Cod, Mass.

ture and release. A bat carried 62 miles by Casteret (1938) was taken 12 miles from its home cave on a direct line with the point of release. A *Myotis l. lucifugus* was transported 168 miles from Roxbury, Conn.



Text fig. 2. Movements of Banded Bats: *Myotis l. lucifugus*
(Arrows indicate direction of flight)

to Chittenden, Vt. and was retaken the next winter at East Dorset, Vt., 118 miles north of Roxbury, Conn. These bats, at least, were apparently traveling directly in the direction of their goal.

These homing experiments seem to satisfy amply the second criterion

TABLE 3. FOREIGN RETURNS OF BANDED BATS I

Bats which flew from one cave to another.

Species	*Sex Number*	*Place Banded*	*Date Banded*	*Place Retaken*	*Date Retaken*	*Distance*	*Direction of Flight*
Myotis lucifugus lucifugus	38-60869	Roxbury, Ct.	Apr., 1937	Ancram, N. Y.	Feb., 1938	37 miles	N.N.W.
" "	H45482	Chester, Mass.	Feb., 1937	Roxbury, Ct.	Apr., 1937	55 "	S. × W.
" "	H42723	E. Dorset, Vt.	Apr., 1936	Chittenden, Vt.	Apr., 1938	35 "	N. × E.
" "	38-24806	S. Bethlehem, N. Y.	Nov., 1937	Chittenden, Vt.	Apr., 1938	120 "	N.E.
Myotis sodalis	H40997	E. Dorset, Vt.	Nov., 1934	Plymouth, Vt.	Nov., 1935	28 "	N.E.
" "	H40878	" " "	" "	" "	Dec., 1935	28 "	N.E.
" "	H40891	" " "	" "	" "	Apr., 1937	28 "	N.E.
" "	H42593	" " "	Apr., 1936	Roxbury, Ct.	Apr., 1937	135 "	S.
" "	38-25211	" " "	Apr., 1937	" "	Apr., 1938	135 "	S.
" "	38-25290	" " "	Apr., 1937	" "	Feb., 1938	135 "	S.
" "	H42249	Chittenden, Vt.	Nov., 1935	Plymouth, Vt.	Nov., 1936	21 "	S.E.
" "	H42413	" "	Nov., 1935	E. Dorset, Vt.	" "	35 "	S. × W.
" "	37-60124	" "	Apr., 1937	Ancram, N. Y.	Feb., 1938	142 "	S. × W.
Myotis keenii	H45413	Chester, Mass.	Feb., 1937	Roxbury, Ct.	Apr., 1937	55 "	S. × W.

advanced above as indicating migratory habits; there can be little doubt that the cave bats have a well developed homing instinct.

(c) *Foreign Returns.*

The recapture of banded bats which have actually migrated constitutes the most satisfactory type of evidence which we can hope to obtain. As mentioned above, the *Myotis l. lucifugus* at summer colonies on Cape Cod, Mass. move occasionally from one building to another. But since these colonies are only five miles apart, occasional shifts are not surprising. Bats are less likely to move voluntarily from one cave to another, and only 8 have been recorded as foreign returns (excluding the atypical E. Dorset colony for reasons explained in footnote 2, page 230) as compared with 979 which have been taken as local returns. These 14 foreign returns from cave to cave present no unified picture and, with one possible exception mentioned below, they are probably the result of occasional random wanderings. Eisentraut (1936) likewise found that out of 6000 cave bats (mostly *Myotis myotis*) banded in two caves 26 miles apart, only 0.2% moved voluntarily from one cave to the other. Table 3 shows the details of these flights from one cave to another.

No less than 102 (1.8%) of the 5657 *Myotis myotis* banded by Eisentraut (1936) in caves near Berlin were retaken during the summer, almost all at points to the north and east of the caves where they were banded. The distances between caves and summer colonies ranged from one half to 100 miles.

Text fig. 2 shows the points of banding and recapture of the seven foreign returns of *Myotis l. lucifugus* which have been obtained between caves and summer colonies, and Table 4 gives these returns in tabular form. In most cases the summer colony was north or east of the cave, as would be expected in New England since the large caveless areas are near the coast while the limestone belt containing all of the caves is on the western border of the district. The longest distance which a cave bat has been definitely traced by the recovery of a banded individual is 168 miles (Mashpee, Mass. to East Dorset, Vt.).

One other foreign return should be mentioned here. A *Myotis l. lucifugus* banded at South Bethlehem, N. Y. in November 1937 was retaken at Chittenden, Vt. on April 10, 1938, having flown northeastward 120 miles during the interval. Perhaps this bat was beginning his spring migration in early April by moving from cave to cave during brief spells of warm weather. This flight is shown by a broken line in Text fig. 2. Bats bearing bands numbered H45482 and H45413 also flew 55 miles from one cave to another during the winter months.

TABLE 4. FOREIGN RETURNS OF BANDED BATS II

Bats which migrated from cave to summer colony or vice versa.

Species	*Sex Number*	*Place Banded*	*Type of Colony*	*Date Banded*	*Place Retaken*	*Type of Colony*	*Date Retaken*	*Distance Flown*	*Direction of Flight*
Myotis lucifugus lucifugus	H43269	Mashpee, Mass.	Summer	June, 1936	Roxbury, Ct.	Cave	Nov., 1937	160 miles	W.
" "	H43413	Cotuit, Mass.	"	July, 1936	E. Dorset, Vt.	"	Nov., 1936	169 "	N.W.
" "	H43617	Mashpee, Mass.	"	July, 1936	E. Dorset, Vt.	"	Nov., 1936	168 "	N.W.
" "	H43664	Mashpee, Mass.	"	Aug., 1936	E. Dorset, Vt.	"	Apr., 1937	168 "	N.W.
" "	H46232	Mashpee, Mass.	"	July, 1937	E. Dorset, Vt.	"	Dec., 1937	168 "	N.W.
" "	H43579	Lake Bomoseen, Vermont	"	July, 1936	E. Dorset, Vt.	"	Nov., 1938	28 "	S. × E.
" "	H43755	Hubbardton, Vt.	"	Sept., 1936	Roxbury, Ct.	"	Apr., 1937	155 "	S.
" "	37-709898	Salisbury, Conn.	Cave	Apr., 1937	Rider's Mills, New York	Summer	Aug., 1937	30 "	N.N.W.
" "	38-25354	E. Dorset, Vt.	Cave	Dec., 1937	Henniker, N. H.	"	? 1938	62 "	E.N.E.
Myotis sodalis	38-25282	E. Dorset, Vt.	"	Dec., 1937	Shaftsbury, Vt.	"	May, 1938	20 "	S.
Pipistrellus subflavus	37-60815	Sheffield, Mass.	"	Apr., 1937	Katonah, N. Y.	"	? 1938	85 "	S.S.W.

One big brown bat, *Eptesicus f. fuscus,* banded during hibernation in a mine at Roxbury, Conn. was retaken the following summer at Washington, Conn. about 10 miles to the northwest. This one record is consistent with the assumption, justified above on other grounds, that this species does not migrate long distances.

These foreign returns are too few in number to prove anything conclusive about the New England bat population as a whole, for they might represent atypical cases. Nevertheless it is certain that even the small cave bats do sometimes fly several hundred miles to reach suitable caves for their hibernation. Thus it is not necessary to assume that cave bats must be able to hibernate outside of caves, simply because they are found in summer in regions where caves do not exist. It is quite possible that the majority of the banded bats migrated much farther than those recovered, and spent one season entirely outside of the area studied. I feel reasonably sure that there are few good bat caves in western New England, which I have not visited. If the bats I have banded in New England summer colonies do hibernate in caves in this area it is surprising that so few have been retaken. During the next year or two, while most of these bats are still alive, naturalists in neighboring states and provinces have a unique opportunity to secure some extremely significant returns by searching caves and summer colonies for banded bats.

Summary and Conclusions

In the United States the tree bats (*Lasiurus borealis, Lasiurus cinereus* and *Lasionycteris noctivagans*), which do not normally hibernate, fly south from their breeding range in northern United States and Canada to the southern States where insect food is available throughout the year. The hoary bat[1] probably flies regularly to Bermuda and the other two tree bats may sometimes do so.

The big brown bat, *Eptesicus f. fuscus,* is very hardy and can apparently hibernate outside of caves even in winter climates as severe as those of New England and Minnesota. There is little evidence that it migrates any great distance, but it has a definite homing instinct when transported 19 or 20 miles from its home roost.

Recoveries of banded bats have shown conclusively that during the winter months *Myotis l. lucifugus* and *Myotis keenii septentrionalis* occasionally travel as far as 120 miles from one cave to another.

[1]*Lasiurus cinereus.*

The smaller cave bats (genera *Myotis* and *Pipistrellus*) have a strong homing instinct when released up to 50 miles from the point where they were taken, and some have returned when transported as much as 156 miles. These species probably return in winter to caves even though this may involve a migration of 150 to 200 miles from their summer range. Two species of *Myotis*, in Europe and in New England, have been definitely traced by recoveries of banded individuals from caves to summer colonies as much as 166 miles apart.

The evidence available, taken as a whole, is sufficient to indicate very strongly that bats of several genera in both Europe and North America perform annual migrations as extensive as those of many migratory birds.

APPENDIX I.

A method of analysing local returns of banded bats

The following is a very simple statistical consideration of the banded bats retaken at the place of banding during subsequent seasons. It is possible under certain conditions to compute the number actually returning to a colony from the percentage retaken. This treatment could perhaps be profitably applied to the local returns obtained by marking birds or other animals.

> Consider a population of bats wintering in a cave, and assume that the population is constant, that is: the annual mortality of adult bats equals the number of young surviving until winter.

Call F the fraction of the bats banded one winter which *return* the next winter to the cave under consideration.

Call P the fraction of the bats banded the first year which are *retaken* at the cave the next season.

Call S_a the fraction of the bats banded (adults) which *survive* until the next winter.

Call C_1 the fraction of all the bats present which are banded the first winter.

Call C_2 the fraction of the bats present which are caught the second winter.

Call Y the average number of bats born each year per adult.
and
Call Sy the fraction of the young born which survive until winter.

Now obviously, if all the bats still alive return to the cave:	$F = Sa$
and if all bats present are caught on each visit:	$C_1 = C_2 = 1$
and	$P = F = Sa$
but in the general case where C_1 & $C_2 \neq 1$ (some bats not caught)	$P = C_1 C_2 F = C_1 C_2 Sa$
Since the total population is constant:	$Sa = 1 - YSy$
therefore if all surviving bats return to the same cave the next winter:	$P = C_1 C_2 (1 - YSy)$
or in the general case:	$P = F C_1 C_2 (1 - YSy)$
Ordinarily $C_1 = C_2$ (on the average) so that we may write:	$P = F C_1^2 (1 - YSy)$

The quantities C_1, C_2, Y and Sy can be estimated and a maximum value for P be thus obtained which will be the fraction we might expect to recapture if all surviving bats returned to the cave where they were banded (i. e. f=1).

For *Myotis l. lucifugus* Y is probably 0.5 (one young per year assuming monogamy and assuming that all adults breed). C_1 & C_2 vary with the cave, probably being about 0.95 at a small cave like the one near Plymouth, Vt., and perhaps about 0.7 at a large mine like the one at Roxbury, Conn. Sy is the most questionable of all, but a value of 0.7 seems a fair approximation considering what a "safe" life the bats lead.

Substituting these admittedly conjectural values we obtain:

For Plymouth, Vt. cave:	$P = F \times (0.95)^2 (1 - 0.5 \times 0.7) = 0.585\ F$
actual value for P at Plymouth cave was:	$P = 0.568$
	$F = \dfrac{0.568}{0.585} = 0.97$
For Roxbury, Conn. mine:	$P = F \times 0.7^2 (1 - 0.5 \times 0.7) = 0.32\ F$

actual value: $P=0.31$

$\therefore$ $F=0.97$

(i.e. $F=$approximately 1, or all surviving bats returned to these caves).

However, not all colonies yielded return percentages so nearly coinciding with the estimated values for P obtained by setting F equal to 1.

These considerations, not obvious at first glance, show that even recovery percentages as low as 30% may indicate an almost perfect tendency for bats to return to a colony successive seasons. This may

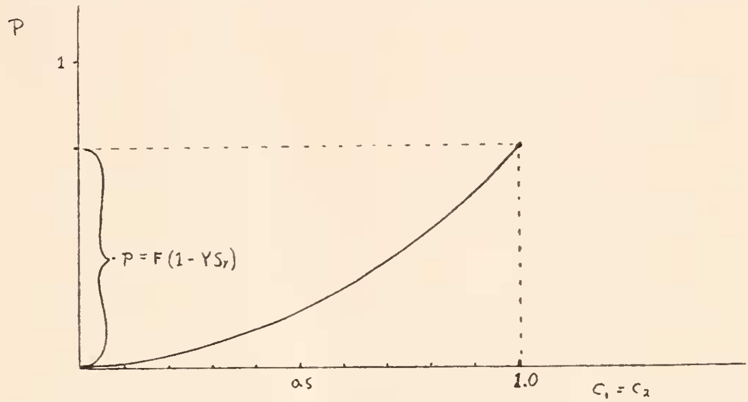


Fig. 3. Theoretical relation between P and C_1; other variables constant.

be represented graphically by plotting P against $C_1=C_2$, holding the other variables constant so as to obtain a simple function. Such a curve is shown below, and it enables one to visualize graphically the fact that P, the percentage retaken, varies as the *square* of C_1 and hence approaches a constant value, distinctly less than 1 as C_1 approaches unity.

It is not claimed that the actual figures here presented are consistant, typical or significant, nor that the estimated values for such quantities as Sy are anything but rough approximations. The main purpose of this treatment is to present a method of analysing the data obtained from local returns so that the critical factors may be appreciated and the fullest possible significance may be perceived in whatever data may be available.

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